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RELATIONSHIP OF THE REPRODUCTION OF THE TOBACCO MOSAIC VIRUS TO THE STAGE OF DEVELOPMENT OF THE PLANT-HOST

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[NOTE: Numbers in parentheses refer to the bibliography. Tables referred to herein are appended at the end of this publication.]

The metabolism occurring in a cell protoplasm constantly changes the material basis of the growth and development of organisms. The process of development, a formation of quantitively varying conditions of cells or tissues, effects the changeability of metabolism processes and leads to a change in the material basis of life itself. These regularly occurring changes in metabolism characterize the various stages of ontogenesis, the value of which is shown in the well-known theory of stage development in plants.

Academician T. D. Lysenko's ideas were quickly acclaimed by Soviet fermentologists, and biochemical indices were established for the variable tendencies of the enzymic processes in developing plants. In this connection, A. L. Kursanov writes: "In the light of T. D. Lysenko's data on the theory of stage development, research on the internal biochemical activity of an organism throughout its entire life cycle acquires a particular interest and value." (2)

The enzymic processes occurring in a protoplasm form one of the most important factors in metabolism, growth, and development. All the most important syntheses in a cell, among them the albumin synthesis which consists of the main part of the protoplasm, take place on this basis.

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Considering virus albumin as the transmissive albumin in a protoplasm, we cannot escape the conviction that the synthesis of their molecules in infected cells is also subject to the metabolism system of a plant, and that the speed of virus reproduction alters in relation to changes in this system normally connected with plants undergoing stage development.

The attachment of phytopathogenic virus to the nucleoprotein group establishes the place of their synthesis in the fermentative system of a cell.

It is known that the introduction of a negligible quantity of the nucleoprotein virus of a tobacco mosaic into a cell of a sensitive plant leads to the rapid accumulation of a new mass of the virus substance. This accumulation occurs as a result of the reporduction of virus molecules; however, at present the mechanism of this reproduction is not known.

Nevertheless, it is scarcely possible to imagine the rapid growth of a complex albumin virus substance taking place without the participation of the synthetic action of plant-host proteases or of proteases which lead to a system of virus molecules the existence of which is hypothetically admissable.

For our working hypothesis we assume that the formation of virus albumin, as in the case of any albuminous body originating in a living protoplasm, takes place with the assistance of the synthetic action of proteases, and is subject to the general laws pertaining to fermentative reactions of this type.

This assumption indicates our first problem, which is the establishment of a correlation between the speed of reproduction of virus albumin and the synthetic action of plant-host proteases. The results of our experimental research are given below.

Method

The object used in the experiments was the hybrid Nicotiana glutinosa X Nicotiana tabacum prepared by Professor Ternovskiy. This hybrid does not differ in any of its main features from the normal Turkish smoking tobacco, but has one characteristic of N glutinosa: when infected with tobacco mosaic virus it does not show the symptoms of general sickness of the mosaic which are usual in ordinary tobacco, but indicates a local reaction by the formation of small local necroses on its leaves at points of infection.

An unusual feature of our method was the use of the necrotic reaction of hybrid tobacco for determining the speed of reproduction of tobacco mosaic virus.

This use of the necrotic reaction is soundly based. In 1933, Jensen (6) proved that virus reporduction takes place in sections of tissue where local necrosis has formed on the second and third day after infection. Extracting virus from separate necroses, this author induced up to ten consecutive transfers of virus on the N glutinosa and obtained normally developed necrosis in each case. If the virus had not multiplied in the tissues before the necrotization, it would have been so thinned out in the final transfers that it would have lacked the necessary concentration required to induce infection in the tobacco.

Jansen's conclusions are a basic condition in our method.

However, we tried to use necroses not so much for qualitative as for quantitative analysis. Our basic methodical conclusions can be stated as follows:

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1. With identical concentration and action of a virus extract used during infection, the quantity of necroses on a hybrid leaf is proportional to the quantity of cells whose physiological composition permits the reproduction of virus in them.

2. The speed of reproduction of virus particles can be judged by the speed of appearance and the growth of necroses in diameter, because these effects are directly related to one another.

The first assumption is self-evident. If, for example, we take two leaves from different parts of the same plant and infect them by identical means with the same virus extract, and then obtain in them sharp differences in the quantity of necroses induced, we are entitled to assume that there were more cells in which the virus found conditions suitable for reproduction in the leaf which had the greater quantity of necroses at the time of infection. It is evident that there would be fewer such cells in the leaf with the smaller quantity of necroses; therefore, the virus molecules which fell on them during infection would remain neutral and would be obstructed at the moment of subsequent death of those isolated destroyed cells which form the primary sources of infection.

The second assumption concerning the connection between the speed of appearance and growth of necroses and the speed of virus reproduction is also well founded. Necrosis fixes the area of virus diffusion in tissue, and consequently the size of its radius determines the distance to which the virus can extend from the primary point of infection. It is evident that if this distance is different, for the same time interval, in two halves of the same leaf subjected to dissimilar conditions, we are entitled to conclude that it was the difference in conditions which led to the different speed of extension of the virus particles, and that in one case this extension occurred more slowly and in the other case, more quickly.

The concealed species of a tobacco mosaic virus is reproduced more slowly than the normal species, and as Jensen (7) showed, it induces finer necroses than the latter in leaves of the N glutinosa.

In the case in point, the size of necrosis was directly related to the speed of reproduction of two related species. Another species of the same virus, called No 104 by Jensen, not only induced considerably finer necroses than the normal species but also required more time for their development. Works by Woods (12) and Ryshkov and Sukhov (4) have shown that the suppression of virus reproduction in cells of a hybrid or N glutinosa leaf by using certain substances leads to a simultaneous suppression of the necrotic reaction. Necroses are either developed or are formed late, in small numbers and size. Optimum conditions for virus reproduction also govern the maximum dimensions of necroses. We will show later to what extent the conditions of virus reproduction can affect the size of necroses in hybrid tobacco.

The necrotization of hybrid tobacco cells takes place as a result of the accumulation of virus molecules in the cells up to the concentration required to produce a lethal effect. The size of necrosis depends on the speed of virus diffusion in the tissues; the larger the latter, the larger the area of tissue the virus will cover before it is obstructed by dead cells. It is known that the speed of diffusion of solutions is directly proportional to their concentrations. We can therefore say that the speed of diffusion of virus molecules in the protoplasm is directly proportional to the concentration of virus molecules. But since the virus molecules penetrating into new cells continue to multiply in their turn, a flexible relationship is

established between the speed of diffusion of initial molecules and the supplementary speed of their concentration on account of reproduction. This relationship stipulates a definite level of diffusion in those sections of a cell most widely separated from the initial points of infection.

Finally, the death of tissue at a particular moment halts the diffusion of the virus, and, since the virus cannot extend through dead cells, the growth of necrosis is stopped and the outlines of the area of virus diffusion become clearly defined. It is evident that virus diffusion does in fact take place from the primary center because the necroses have quite a regular rounded form and often give the appearance of concentric rings, which indicates the rhythmic nature of the process.

The use of necrotic reaction in the study of the speed of virus reproduction in a tobacco mosaic has a number of advantages when compared with the study of this problem in ordinary tobacco showing general infection.

Necroses appear very quickly, which means that the solution to an experiment can be obtained in the course of 3 or 4 days.

As a result of local reaction, necroses do not substantially disturb the normal physiology of the plant as a complete organism. This is extremely important in the correct evaluation of effects connected with the directivity of fermentative processes in the tissues and organs of the host.

On the other hand, parallel control experiments show that in the first days after inoculation the laws of virus reproduction remain the same both for the cells of ordinary tobacco subsequently reacting to general infection and for cells of hybrid tobacco where the infection is local. This permits the conclusion that for small infected areas of tissue in the hybrid, virus reproduction conforms to type, and the final result, necrosis, serves as an index for the degree and speed of this process.

Our work was made considerably easier by the fact that tobacco has long been the object of extensive biochemical research. In particular, the problem of the nitrogen and albumin balance in tobacco plants has been studied in detail by Smirnov, Kreve, Mothes, Shultze, and Spencer. These authors, together with Kudryavtsev and Prozorovskaya, have also made a special study of the synthetic action of proteases in tobacco plants.

Finally, the large number of works produced from the Institute of Biochemistry, Academy of Sciences of the USSR, by Academicians Oparin, Kursanov, Sisakyan, and others were a valuable contribution to our research and furnished extensive material on the problem of directivity of fermentative processes in living plant tissues.

Experimental Part

It is known that the synthetic action of proteases in tobacco leaves is subjected to substantial changes dependent upon the stage of plant ontogenesis, the position of the leaf on the stalk, the age of the leaf, the topography of the leaf, and, finally, a number of outside factors such as temperature, fertility of earth, etc.

In our experiments we tested the speed of reproduction of tobacco mosaic virus in hybrid tobacco leaves using stages and conditions of development already approved for tobacco plants by biochemists engaged in the study of hydrogen and albumin balance and the synthetic action of proteases.

It appeared that the speed of virus reproduction was directly related

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to the action of host proteases. If a young hybrid plant is taken and all its leaves are uniformly inoculated with virus extract, the quantity of necroses and their size will be different at various levels. The maximum development of necroses will occur at certain middle levels, whereas the highest and lowest leaves will show a smaller number of necroses (Table 1).

Below, we give research data on hybrid plants. At the moment of inoculation, one group was in the blossoming phase and the other in the seed-ripening phase. The leaves of plants in both groups were inoculated simultaneously with the same virus extract. Table 2 shows the average quantity of necroses per half leaf.

Our attention was drawn to the predominance of necroses at all levels of the blossoming plants in comparison with those in the ripening phase. The qualitative difference between the reactions of both groups was shown by the fact that several of the highest levels of the ripening plants had practically no necroses. In spite of the fact that these leaves were alive, and remained on the bush for a long time after the experiment, the virus could not reproduce in them. With regard to certain of the higher levels, the differences were also very great.

Figure 1 [not reproduced] gives a graphical representation of the percentage relation of the quantity of necroses to plant levels in various stages of development. The quantity of necroses above level II is taken as 100 percent in each case.

For a young seedling, a steep, single-peak curve is characteristic, the highest point of which corresponds to one of the middle leaf levels. In the more mature stages of hybrid tobacco development, the curve invariably has a number of peaks which characterize the reaction periodicity. Levels of leaves reacting to inoculation by showing an increased number of necroses alternate with levels whose leaves form a comparatively small number of necroses. This periodicity in the capacity of leaves at different levels to achieve a varying degree of virus reproduction reflects the periodicity, peculiar to plants, of directivity of fermentative processes which has been mentioned by Nilov and Pavlenko (3).

These connections in the number of necroses on leaves at different levels were subjected to changes in the process of plant ontogenesis.

In the comparatively early stages of ontogenesis, the lowest leaves formed a relatively large number of necroses, but towards the budding and blossoming period the number of necroses on them fell sharply and a series of consecutively more highly positioned leaf levels were similarly affected. This result is in complete agreement with literary data on the reduction of the synthetic action of proteases in sprouting tobacco leaves at blossom time. The predominance of hydrolytic disentegration processes in albumin over those of synthesis reaches its highest point at this period. Towards the end of blossoming and during the period of seed-ripening the leaves with the largest number of necroses are concentrated at the top of the stem. At this time, the majority of levels only give a weak necrotic reaction to the injection of virus. At other times they behave normally and conform to the high inherent synthetic action of proteases in them by energetically reacting to virus and forming a large number of necroses.

The capacity of leaves at any level to react with necroses to virus injection can be varied experimentally. We carried out the following experiment. On 23 August we took 40 hybrid plants, approximately identical in size, which were in the prebudding stage and which had 14-16 levels of leaves. Twenty plants were established as controls and their leaves marked at level III; in the remaining 20 plants all the leaves and buds were removed except

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for the leaf in level III (counting from the top).

The growth cone and a few embryonic upper leaflets were also left. The remaining single leaves quickly surpassed the corresponding leaves on the control with regard to size. They became thicker and more darkly colored. On 9 September, we inoculated the 20 experimental and the 20 control leaves with the same virus extract. At this time the marked leaf on the control corresponded to level XIV-XV. A count of the induced necroses, made on 13 September, showed that in the majority of experimental leaves the necroses were far larger and more numerous than in the control leaves (Table 3).

However, when the single leaves of a lower level were used in another experiment, the corresponding reaction in the form of an increase in the number of necroses did not occur.

When considering the results of the inoculation of leaves at various levels, we were surprised to find several cases of the complete or almost complete absence of necroses. This was only observed in certain of the mature lower leaves. It was evident that they contained practically no cells in a suitable condition for virus reproduction. As is already known, the synthetic action of proteases in these leaves is reduced to a minimum and their hydrolytic action is predominant. Hence, it is easy to understand how difficult it would be to produce suitable conditions for virus synthesis in vitro, when even the living protoplasm of a sensitive plant cannot do it.

In the following experiment we examined the comparative development of necroses in conditions of reduced and increased hydrolysis.

Half leaves of hybrid plants growing in the hothouse were cut up and left to starve; their corresponding halves, together with the central vein, were left on the plant. After 7 days these and the other halves were inoculated with virus extract and the isolated halves were then placed in a darkened hothouse together with the experimental plants and consequently were subjected to the same temperature conditions. The famine system of starvation increased the hydrolytic disintegration of albumin in the leaf tissues, the smallest effect of this process being obtained in the most mature leaves. This result confirmed our expectations. Starvation led to a sharp decline in the number of necroses in the corresponding halves of the leaves. The necroses appeared 24 hours later than in the control (the halves remaining on the plants). There were considerably fewer necroses in the mature starved halves than in the control. The form of the necroses was also changed. In the mature leaves they often appeared not rounded, but star-shaped or striped. This can probably be explained by the fact that the virus molecules extending on all sides from the initial center did not find suitable conditions for synthesis at many points on the starved leaf. Deformation therefore resulted because necrosis only occurs along those diffusion channels for virus particles in which multiplication takes place and leads to an increase in virus concentration and the subsequent death of cells.

We later noticed that deformation of necroses is also not uncommon under natural conditions in fading leaves on the lowest levels.

The starvation experiments showed that strong hydrolysis, overcoming the synthetic processes in tissues, reduces the speed of virus reproduction. In conditions of nitrogen starvation, the composition of the hybrid plant produces this result. The quantity and size of necroses in plants lacking nitrogen is lower than that in normal plants.

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Relation of Virus Reproduction in a Tobacco Mosaic to the Age and Topography of the Inoculated Hybrid Leaf

It is known that the synthetic action of proteases varies widely in relation to leaf topography. Pearsall and Billimoria (8) found a large predominance of the synthetic action of proteases in isolated narcissus leaves at the basal part in comparison with that at the top. According to Sisakyan and Kobyakova (5), a considerable difference in the synthetic action of proteases in relation to various parts of a leaf was observed in sunflowers. In their experiments, the basal part of a leaf in level III, measured from the bottom, showed a protease action seven times greater than that at the top. Albumin synthesis, generally speaking, was not observed in the central part of the leaf. In the sixth leaf from the bottom these differences were somewhat reduced, but still remained noticeable. In this case synthesis was observed in the central part of the leaf. Finally, in the tenth leaf from the bottom, albumin synthesis in the basal part did not noticeably exceed that in the top and occurred normally in the central part.

Taking into account the relation of virus accumulation to the synthetic action of proteases, we turned our attention to the significance of leaf topography in the reproduction of virus particles. Sadasavian's data (9) has some bearing on this, because, although his work was not directly connected with research on the connection between albumin synthesis and virus reproduction, he produced all the material showing the effect of leaf topography on virus titer (Table 4).

From this data it is evident that the virus titer of the aucuba mosaic fell particularly quickly in the central part of the leaf, much more slowly in its base, and attained its maximum in the top part. This result deserves considerable attention in the light of biochemical data on the differences in albumin synthesis related to leaf topography.

Guided by data from Kudryavtseva and Prozorovskaya on the synthetic action of proteases in healthy tobacco leaves at various levels, we investigated corresponding changes in the degree of virus reproduction in the tobacco mosaic in various parts of hybrid tobacco leaves.

According to Kudryavtseva and Prozorovskaya, the synthetic action of proteases in the uppermost tobacco leaves is reduced to a minimum, but increases in the more mature leaves at the middle levels. Hence we may conclude that the action of proteases in the uppermost leaves is particularly small at the base in the region of the youngest tissue, and increases in the top part of the leaf where the more mature tissue is found. In fact, as was shown in experiments, the inoculation of the uppermost leaves of young hybrid tobacco plants usually showed a clear differentiation both in quantity and the size of necroses. The basic mass of necroses occurred in the upper half of the leaf. In the lower half, there were either almost no necroses or they were very much finer. Cases often occurred where the lower half showed minute spots which only revealed the characteristic necroses structure when viewed under a microscope.

The relation varied in the lower levels. The differentiation in size and extent of necroses was reduced or even disappeared, but it again became noticeable in some of the lower-middle levels. In these cases, in contradiction to the condition observed in the uppermost leaves, the largest number of necroses occurred in the lower half of the leaf and their size appeared greatest at the base (Table 5).

From the point of view of the synthetic action of proteases, this result is understandable because the reduction of synthesis in a mature leaf is probably more noticeable in the old tissue at the top than in the younger tissue at the base. It must however be emphasized that in plant development all

these relations are very flexible and depend not only on the level of the leaf but also on the age of the plant and on its ontogenetic stage. Table 5 shows the monotypic reaction of hybrid tobacco plants to the inoculation of a leaf in the XI-XII level (measured from the top). Out of a total of 13 plants of the same age, there was only one case where there was no differentiation between the sizes of necroses in different parts of the leaf. In 12 cases this differentiation was clearly shown. The largest necroses were found at the base of the leaf, finer ones in the central part, and the finest at the top. The nature of these necroses is shown in Figure 2 [not reproduced].

The general laws governing the size and location of necroses in relation to leaf topography at different levels, particularly when compared with analyses by Kudryavtseva and Prozorovskaya, convince us that it is highly probable that our ideas are correct concerning the correlation between the synthetic action of proteases in the plant host and the accumulation of virus albumin.

Cases of gradual changes in the size of necroses at the base and top of a leaf in relation to the leaf level are shown in Table 6.

Anomalous Parallel Movement of the Synthetic Action of Proteases

As we showed above, the small upper leaves of the hybrid have fewer necroses than those situated lower down; this is in accordance with the correlation of the synthetic action of proteases. However, literary data shows that virus accumulation in a tobacco mosaic in most intense in these same upper leaves. Experiments showed that this contradiction is a fact.

We tested the speed of virus accumulation in the uppermost and central leaves of ordinary tobacco, titrating the virus on the fourth day after inoculation, i.e., long before the appearance of symptoms of general sickness.

It turned out that in this case, virus accumulation in ordinary tobacco leaves follows the same law as in the hybrid, i.e., the virus accumulates more quickly in the central levels than in the upper levels. On titration of hybrid leaves, the extract from inoculated upper leaves gave an average of 26.4 necroses in ten samples, while the extract from the central leaves gave 104.7 necroses, or four times as much. A similar result was obtained by Sadasivan in 1940.

This same author showed that later, after the appearance of mosaic symptoms, the relation is reversed and the virus concentration in the upper leaves becomes higher than that in the middle and lower leaves.

Kudryavtseva and Prozorovskaya (1) determined the action of proteases in tobacco leaves 15-20 days after mosaic development. Using Kursanov's and Bryushkova's method, they established that the upper leaves of healthy tobacco do not show to any perceptible extent the synthetic action of proteases so noticeable in the leaves at the central levels. On the other hand, the reverse is true in mosaic plants where the greatest action of proteases was observed in these same upper leaves.

Comparing our data with that of Kudryavtseva, Prozorovskaya, and Sadasivan, we conclude that with a long-standing mosaic disease in tobacco, the synthetic action of proteases occurs in organs not normally affected in healthy plants, and that it is of particular significance that a simultaneous formation occurs, in these same organs, of an increased virus reproduction, which, until that time, was limited to the central levels.

In this case the direct connection between the synthetic action of plant

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proteases and the speed of virus synthesis is sharply underlined by the sickly, distorted physiology of the mosaic plant.

Discussion of Results

Our data shows that in all those cases where the biochemists indicated a noticeable difference in the synthetic action of proteases for tobacco tissue we invariably find that virus albumin synthesis increases when the albumin synthesis in the host increases; conversely, in tissues with a predominance of hydrolytic albumin disintegration, virus synthesis is either impossible or is retarded. Even in the case of a pathological variation where general disease of the tobacco mosaic alters the course of synthetic processes and induces them in organs not normally affected in healthy plants, the processes of virus albumin reproduction are shifted to these same organs, although their basic reproduction is completed in another part before the disruption of the normal physiology of the plant.

The comparison of all results convinces us that, as might be expected, virus albumin synthesis is related to the synthetic action of proteases.

The question arises as to which proteases synthesize the virus particles, the plant-host proteases or the proteases inherent in the virus molecules themselves.

Discussion of this question can only be carried out using circumstantial data. The accumulated scientific data on viruses convinces us more and more that virus albumin is produced by its own synthetic action. We have some very strong arguments in support of this theory.

It is possible to destroy a tobacco plant by more than 110 different viruses or their subspecies. In each case, we should be able to assume the ability of tobacco protease to synthesize each of these different albumin viruses although many of them are not only hostile to the plant, but even destructive.

This assumption is, however, improbable, because the formation of combinations of organisms which facilitate the construction and strengthening of conditions which bring about the death of the carriers themselves is not possible. Where possible, a plant attempts to free itself from the hostile and destructive substance, or tries to neutralize it. For example, tobacco infected with ring-spot virus gradually recovers from the disease. With the aid of an analytical ultracentrifuge, Stanley (11) showed that virus reproduction in convalescent tobacco tissue decreases sharply. If a portion of fresh virus is introduced into a convalescent plant, its reproduction is suppressed.

Finally, if a virus particle is the product of plant protease synthesis, it would be natural to expect its hydrolytic disintegration during a change in the protease action of the host on its hydrolysis. However Spencer's circumstantial research (10) shows that virus albumin is not disintegrated even in conditions of the strongest hydrolysis which occurs in aging or starving tissues, i.e., virus albumin behaves as a hostile substance have no points of application for the hydrolytic action of the host proteases.

If, on the other hand, we assume that a virus molecule itself is able to synthesize similar particles from some substrate in the host protoplasm, it is then possible to explain the many peculiarities in its behavior.

A virus molecule, as a nucleoprotein molecule with a complex chemical composition, probably possesses not one but several fermentative functions which ensure its reproduction.

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It is probable that the reproducing albumin structures normally present in a cell synthesize their own body substance independently. In that case both the virus and the reproducing albumin structures of the protoplasm must, among other peculiarities, possess functions of specific proteases whose action, in time and place, corresponds to a considerable extent with the action of the normal intracell proteases of a plant cell.

We know nothing about the substrate where the virus molecule is formed, although its complex albuminlike composition is open to doubt. It is probable that "multinuclear" virus, which destroys many types of different plant species, is made up of simpler elements than virus which is specific for particular types, because the biochemical community between plant forms and species is increased by the simplification of the structure and chemical composition of substances, which are converted from albumin to polypeptides, peptones, and aminoacetic acid.

The relation of individual viruses to their relevant substrate makes it probable that the laws we established for the tobacco mosaic virus cannot be applied unconditionally to any virus. Conversely, it may be assumed that a specific substrate necessary for reproducing some other virus would be a limiting factor which modified the simple relation of its reproduction to the synthetic action of proteases.

The discovery of a connection between the synthetic action of plant-host proteases and the reproduction of virus albumin is the key to comprehension of the relation of the multiplication of virus particles to the development stage of an infected plant. The formation and disintegration of albumin bodies in a cell indicates far-reaching changes in its active life, inasmuch as albumin bodies are the main carriers of living protoplasm properties.

A trend in the fermentation processes in a cell not only signifies the chemism of reactions, but above all indicates a general change in the metabolism of substances which control such biological effects as the growth and development of an organism. On the one hand, virus albumin, included in cell metabolism by infection, disorganizes this metabolism by inducing deformed pathological trends, and, on the other hand, submits to its operation.

The quantitively different formation of virus necroses in hybrid tobacco tissues not only indicates the rate of production of virus particles but also the physiological composition of plants in relation to their development stage.

Conclusions

1. The virus albumin injected into cells of a sensitive plant is not autonomous; on the contrary, its reproduction is directly controlled by the functional composition of the plant-host, and changes when this composition is changed.

2. Development stages in the plant-host which determine changes in its metabolism control the reproduction of virus albumin. At some stages in plant development virus reproduction is rapid and at others it is retarded or almost completely suppressed.

3. The reproduction of virus albumin is not only related to the development stage of the plant as a whole, but also to the position, age, and topography of individual organs infected by the virus.

4. All these changes in virus reproduction are closely connected with

the directivity of albumin metabolism in the plant-host, both in the direction of synthesis and in the direction of hydrolysis. An experimenter changing the conditions of plant development can affect the speed of virus albumin reproduction.

5. In certain respects the variable behavior of virus albumin in the protoplasm of the plant-host is also characterized by the conformance of normal discrete cell elements to the laws of the development of a plant organism as a whole.

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Table 1. Changes in the Quantity and Size of Necroses in Relation to the Level of Hybrid Leaves

Plant No	Quantity of Necroses (Numerator) and Their Average Diameter (in mm -- denominator) in Leaves at the Following Levels (from top)									
	II	III	IV	V	VI	VII	VIII	IX	X	XI
1	8/1.0	37/1.8	151/2.1	275/2.1	171/2.5	99/2.8	50/2.0	4/1.8	--	--
2	1/1.6	24/1.5	70/1.8	186/2.0	132/2.7	157/2.4	90/1.6	6/1.4	--	--
3	--	22/0.6	87/0.8	94/0.7	56/0.8	51/1.2	26/0.8	48/1.2	67/1.0	63/0.5
4	--	--	122/0.7	80/1.2	25/0.6	84/1.2	73/1.2	47/0.7	10/0.6	--
5	32/1.0	49/2.0	95/2.3	27/1.3	31/1.3	--	--	--	--	--
6	11/1.0	68/1.8	22/1.3	14/1.0	--	--	--	--	--	--

able 2. Changes in the Number of Necroses in Relation to Leaf Level and Phase of Hybrid Tobacco Development

Phase of Plant Development	No of Plants in Experiment	Average Number of Necroses According to Leaf Levels (from top)									
		II	III	IV	V	VI	VII	VIII	IX	X	XI
Blossoming	13	70.0	88.3	65.7	145.6	95.3	165.0	121.1	133.3	149.1	93.3
Pods ripening	5	10	4.8	16.6	11.2	3.2	6.0	5.2	2.4	1.4	0.6

Table 2 (cont'd)

Phase of Plant Development	No of Plants in Experiment	Average Number of Necroses According to Leaf Levels (from top) XII	XIII	XIV	XV	XVI	XVII	XVIII	XIX	XX	XXI
Blossoming	13	96.8	93.4	108.9	46.6	60.8	84.1	33.5	29.5	18.6	17.9
Pods ripening	5	0.4	0.4	0.2	0	0	0	0	0	0	0

Table 3. Change in the Number of Necroses When one Upper Level Leaf Is Left on the Brush. (The average of 20 cases is shown in each column.)

Date of Removal of All Leaves Except One	Date of Inoculation	Date of Count	Average No of Necroses per Half Leaf. Experiment	Control	Average Diam of Necroses (in mm) Experiment	Control	Average Length and Width of a Leaf (in cm) Experiment	Control	Average Height of a Plant (in cm) Experiment	Control
23/VIII	9/IX	13/IX	296.4	56.3	3.7	2.4	40.8/27.1	32.7/20.9	67.0	105.3

Table 4. Change in the Number of Necroses Induced by Aucuba Mosaic Virus in Relation to the Periods of Preliminary Infection of a Leaf by Ordinary Mosaic Virus (Sadasivan, 9)

Incubation Period of Tobacco Mosaic before Injection of Aucuba Mosaic (in days)	No of Necroses Induced by Aucuba Mosaic Virus		
	In the Top of the Leaf	In Center of the Leaf	In the Base of the Leaf
1	1,470	310	1,06[illegible]
2	1,154	100	977
4	975	35	1,052
6	867	8	847
8	713	0	390
10	452	0	140
15	148	0	12

Table 5. Size of Necroses in Various Parts of a Hybrid Leaf at Level XI - XII (from top)

Plant No	Number of Necroses on the Leaf	Average Size of Necroses (in mm)		
		At the Base of the Leaf	In the Center of the Leaf	In the Top Part of the Leaf
1	67	1.8	1.0	1.6
2	40	3.0	1.1	0.6
3	102	3.0	1.8	1.0
4	32	1.7	1.7	1.7
5	43	1.0	0.5	0.5
6	134	3.0	1.0	0.6
7	86	2.5	1.8	1.5
8	71	3.0	1.8	1.0
9	60	3.1	1.2	0.8
10	71	2.0	1.0	0.4
11	195	4.1	2.0	1.1
12	60	2.0	1.0	0.3
13	110	1.9	1.0	0.5

Table 6. Distribution of the Basic Mass of Necroses According to Levels, and Their Average Size (in mm) at the Top (numerator) and Base (denominator) of a Leaf at a Given Level

Plant No	Levels (from the top) II	III	IV	V	VI	VII	VIII
1	Upper quarter of leaf 1.0/0*	Mainly the upper quarter of leaf 1.9/1.4	Mainly the upper half of leaf 2.2/1.7	Over the whole leaf No differences	Over the whole leaf 2.7/2.1	Over the whole leaf No differences	Over the whole leaf No differences
2	No necroses	Mainly the upper third of leaf 1.8/1.5	Mainly the upper two thirds of leaf 2.8/1.9	Over the whole leaf 2.0/3.0	Over the whole leaf No differences	Over the whole leaf No differences	Over the whole leaf 0.7/1.4
3	Upper half of leaf 1.6/0	Mainly the upper half of leaf 1.4/1.0	Mainly the upper half of leaf 2.0/1.4	Over the whole leaf No differences	Over the whole leaf 2.4/3.0	Over the whole leaf 2.0/2.6	Over the whole leaf 1.1/2.6
4	Upper third of leaf 1.0/0	Mainly the upper half of leaf 1.8/2.0	Over the whole leaf No differences	Over the whole leaf No differences	Over the whole leaf 2.5/3.0	Over the whole leaf 2.0/2.6	Mainly the lower half of leaf 2.0/2.6
5	Upper quarter of leaf 1.5/0	Mainly the upper half of leaf 1.9/1.3	Over the whole leaf No differences	Over the whole leaf No differences	Over the whole leaf No differences	Over the whole leaf No differences	Over the whole leaf No differences

* Size of necroses is shown as "0" in cases where they are absent in the remaining lower part of the leaf.